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Bolitoglossa taylori, A New Salamander from Cloud Forest of the Serranía de Pirre, Eastern Panama

BY DAVID B. WAKE,¹ ARDEN H. BRAME, JR.,²
AND CHARLES W. MYERS³

The Serranía de Pirre is a little-known mountain range that extends northward from the Colombian border for a distance of about 35 kilometers into extreme eastern Panama. The results of recent expeditions indicate that several undescribed species of amphibians and reptiles may be endemic to the isolated, luxuriant cloud forest that covers the top of the *serranía* (Myers, 1969, and unpubl. data). One such species is a salamander that resembles members of the South American *adspersa* group of *Bolitoglossa*, especially *B. savagei* from the Sierra Nevada de Santa Marta of north-coastal Colombia and *B. borburata* from the Cordillera de la Costa of Venezuela. We name the Panamanian species in honor of Edward H. Taylor, in recognition and appreciation of his pioneering work on Neotropical salamanders.

ABBREVIATIONS

G.M.L.-C.W.M., Gorgas Memorial Laboratory, field series of C. W. Myers,

¹ Associate Professor of Zoology and Associate Curator, Museum of Vertebrate Zoology, University of California, Berkeley.

² Section of Herpetology, Los Angeles County Museum of Natural History, Los Angeles.

³ Assistant Curator, Department of Herpetology, the American Museum of Natural History; Associate in Herpetology, the University of Kansas Museum of Natural History, Lawrence.

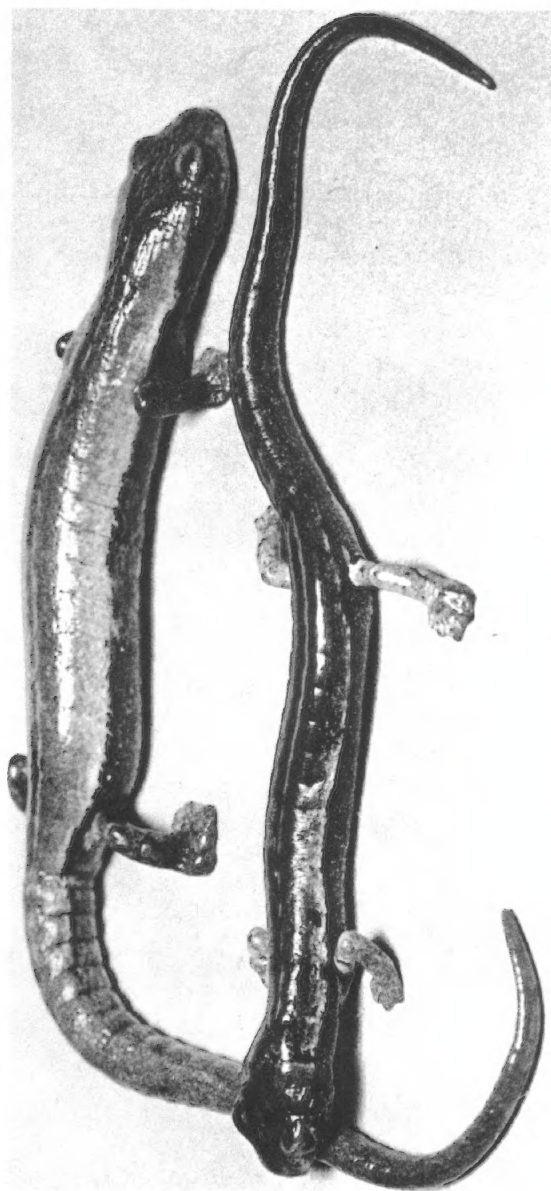


FIG. 1. Paratypes of *Bolitoglossa taylori* photographed in life. Top. Adult female (K.U. No. 116545). Bottom. Adult male (G.M.L.-C.W.M. No. 6077). Approximately $\times 1.5$.

Panama City, Republic of Panama

K.U., University of Kansas Museum of Natural History, Lawrence

L.A.C.M., Los Angeles County Museum of Natural History, Los Angeles

U.M.M.Z., University of Michigan Museum of Zoology, Ann Arbor

***Bolitoglossa taylori*, new species**

Figures 1-3, 4C-E

HOLOTYPE: K.U. No. 116544 (field no. C.W.M. 6075), an adult male, obtained by Charles W. Myers, January 23, 1966 on the south ridge of Cerro Cituro, Serranía de Pirre, at an elevation of approximately 1100 meters (3608 feet), Darién Province, Republic of Panama.

PARATYPES: Twelve specimens, all collected by Charles W. Myers and Tomás Quintero, in the Serranía de Pirre, Darién Province, in May, 1965, and January, 1966. G.M.L.-C.W.M. No. 6077, K.U. Nos. 116540, 116541 (=three juveniles), 116542, 116543, 116545—all with same locality data as holotype. K.U. Nos. 116539, 116546, north ridge of Cerro Cituro, 900-1000 meters (2952-3280 feet) elevation. K.U. No. 116538, north ridge of Cerro Cituro, 960 meters (3149 feet) elevation. K.U. No. 116535, southeast slope of Cerro Pirre, 1440 meters (4723 feet) elevation.

DIAGNOSIS: *Bolitoglossa taylori* is a moderately large salamander (five adult males: 39.5-53.3, mean 46.6 mm.; three adult females: 42.0-64.7, mean 50.8 mm. in standard length¹), with many maxillary teeth (nine specimens: 44-78, mean 60.2) and extensively webbed hands and feet. Tips of the fingers and toes extend slightly from the webbing, except for the first digits. The third finger is longer relative to the others than that in most other members of the genus. Subdigital pads are present, but only weakly developed. This species resembles members of the *adspersa* group (Brame and Wake, 1963). It differs from members of that group as follows: from *B. savagei* in having less rounded and pronounced finger and toe tips, more webbing of hands and feet, less well-developed subterminal pads, and more maxillary and vomerine teeth; from *B. borburata* in having less extensive webbing of hands and feet, a more prominent third finger and toe, subterminal pads, and more vomerine teeth; from *B. pandi* in having more maxillary teeth and slightly more webbing; from *B. capitana* in being much smaller and lighter in coloration; from *B. nicefori* in having less webbing of hands and feet and a narrower head; from *B. hypacra*, *B. valleculea*, and *B. adspersa* in having more extensive

¹ Standard length is the distance from the tip of the snout to the posterior end of the vent. All measurements are of specimens fixed in 10 per cent formalin and stored for more than a year in approximately 70 per cent alcohol.

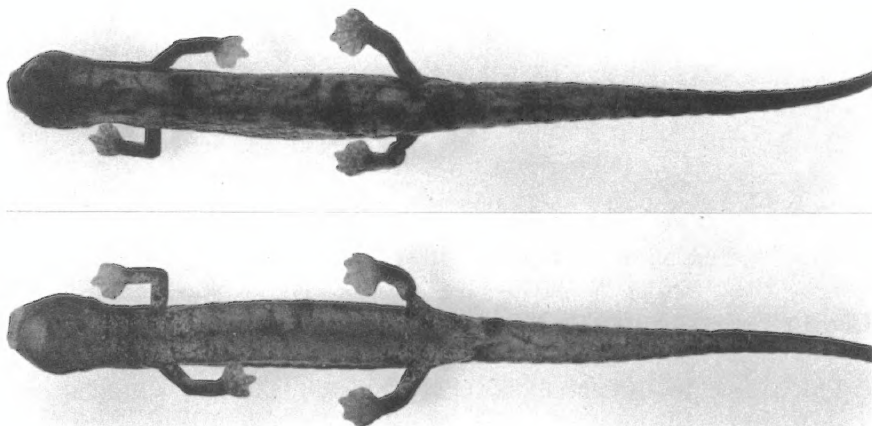


FIG. 2. Holotype of *Bolitoglossa taylori*.

webbing and less well-developed subterminal pads. The only Panamanian species with which *B. taylori* is likely to be confused is *B. biseriata*, a smaller species that has more extensive webbing of the hands and feet, less prominent middle digits, no subterminal pads, and fewer vomerine and maxillary teeth.

DESCRIPTION OF HOLOTYPE: This adult male has a moderately long, somewhat truncate snout and a large (3.9 mm. wide), half-moon-shaped mental hedonic gland. The nostrils are moderately small, and labial protuberances of the nasolabial grooves are moderately large and somewhat flared. The canthus rostralis is moderately long and slightly arched. Standard length is 6.0 times head width and 4.3 times snout to gular fold length. A deep groove below the eye extends for almost the full length of the orbit, following the curvature of the eye, but it does not communicate with the lip. The eyes are moderately small and slightly protuberant. A well-defined postorbital groove extends posteriorly from the eye as a shallow depression for 2.0 mm.; it then proceeds sharply ventrad at the level of the posterior end of the mandible and extends across the gular area as a poorly defined nuchal groove, parallel to, and 4.6 mm. anterior to, the sharply defined gular fold. Vomerine teeth number 32, mostly in single rows that extend just to the outer borders of the internal nares; the rows extend in a very slight curve (nearly a straight line) to near the center of the palate, 0.9 mm. from the parasphenoid tooth patch. Maxillary teeth number 76; they extend posteriorly to a point about five-sixths through the eye. Seven large premaxillary teeth pierce the lip. The tail is moderately constricted at its base. Post-

iliac glands are relatively large and distinct. The limbs are of moderate length and the limb interval is 2. Standard length is 4.0 times the length of the right forelimb, 4.1 times the right hind limb, and 9.2 times the width of the right foot. The webbing of the hands and feet is extensive, with the tips of most digits protruding from the web (fig. 4C-D). Tips of the third finger and third toe extend well beyond the webbing. Sub-terminal pads are present, but are poorly developed. The fingers, in order of decreasing length, are: 3, (2-4), 1; the toes, in order of decreasing length, are: 3, 4, 2, 5, 1.

Measurements (in mm.) are as follows: Head width 8.9; snout to gular fold (head length) 13.3; head depth at posterior angle of jaw 4.1; eyelid length 3.5; eyelid width 2.2; anterior rim of orbit to snout 4.2; horizontal orbital diameter 2.1; interorbital distance 3.7; distance between vomerine teeth and parasphenoid tooth patch 0.9; snout to forelimb 15.8; distance separating internal nares 2.8; distance separating external nares 3.2; snout projection beyond mandible 1.2; snout to posterior angle of vent (standard length) 53.3; snout to anterior angle of vent 48.8; axilla to groin 28.4; tail length 55.9; tail width at base 4.3; tail depth at base 4.2; forelimb length 13.1; hind limb length 12.9; width of right hand 4.5; width of right foot 5.8.

COLORATION OF HOLOTYPE (IN ALCOHOL): This is a colorful salamander with little evidence of a distinct pattern. Golden brown predominates dorsally, with some evidence of a broad dorsal band extending from the back of the head posteriorly onto the tail. This band has markings that range from small spots to connected blotches of darker pigment, approaching black. A grayish stripe, the lateral portion of the indistinct dorsal band, extends from the upper lip and cheek, over the shoulder and limb insertions, onto the tail. Ventral surfaces are much lighter than dorsal or lateral ones. The enlarged mental gland is creamy white. The rest of the throat is a light brownish gray and this color predominates on all ventral surfaces. The ventral color becomes lighter in some regions (near insertion of forelimbs) and darker in others (near middle of belly). Microscopically it can be seen that the ventral pattern results from a sparse reticulum of melanophores that diminishes in some areas and becomes dense in others. In the light areas, the melanophores may be partially overlain, but generally replaced, with a reticulum of cream-yellow chromatophores. Guanophores, mainly single, occur over all ventral surfaces. The posterior half of the tail is uniformly dark brown. Guanophores are present in the lateral stripe and on the eyelids, as well as on the ventral surfaces. Both dorsal and ventral surfaces of the hands and feet are lighter than the grayish limbs.

VARIATION

PRESERVED SPECIMENS: This species is probably sexually dimorphic in size, as are most other members of the genus, with females being larger than males. The largest female is 11.4 mm. longer (21 per cent) than the largest male. The mean sizes of 46.6 mm. and 50.8 mm. standard length, for males and females respectively, are moderate for the genus. Legs are of moderate length, and tend to be slightly longer in males than in females. Hind limb length is from 22.9 to 24.6 (mean 23.6) per cent of standard length in males and from 21.4 to 25.0 (mean 23.3) per cent of standard length in females. Limb interval varies from $1\frac{1}{2}$ to $2\frac{1}{2}$ (mean 2) in males and from 2 to $3\frac{1}{2}$ (mean $2\frac{1}{2}$) in females. Tails are long in both males and females, and are from 3.5 to 28.4 per cent longer than standard length. The heads of both males and females are about equally wide, and standard length ranges from 5.8 to 6.4 (mean 6.1) times head width in the adult sample. The narrowest head and shortest limbs, relative to standard length, are found in the very large female (K.U. No. 116545). Females have more rounded and less truncate snouts than do males. Females have more maxillary and vomerine teeth, relative to size, than do males. Vomerine teeth range in number from 18 to 49 (mean 31) and maxillary teeth range in number from 44 to 78 (mean 60); both are high numbers for the genus.

Structure of the hands and feet is distinctive. Webbing is extensive, but indications of subterminal pads are present. Thus the species bridges the moderate and extensive categories applied to foot structure in *Bolitoglossa* by Wake and Brame (1969). Digits are relatively well defined by cutaneous grooves. The longest digits of both hand and foot tend to be disproportionally long, relative to the others, and often have a rather sharp, inward pointing tip. The largest individual (K.U. No. 116545) differs from all other specimens in having more webbing and less disproportion between the longest and next to longest digits, especially on the feet. The longest digit of the hand in this individual is similar to that of other specimens.

Coloration of this species is as variable as in any member of the genus *Bolitoglossa* that we have studied. Dorsal coloration varies from an almost uniform black with some slightly lighter and some slightly darker mottlings (K.U. Nos. 116539 and 116546) through patterns generally similar to the holotype, to a broad, relatively unmarked cream to golden brown dorsal stripe (K.U. No. 116545) (see fig. 3A). The three juveniles are generally dark gray, mottled with different shades of brownish and blackish gray. Lateral gray stripes are usually present, but they are obscure in

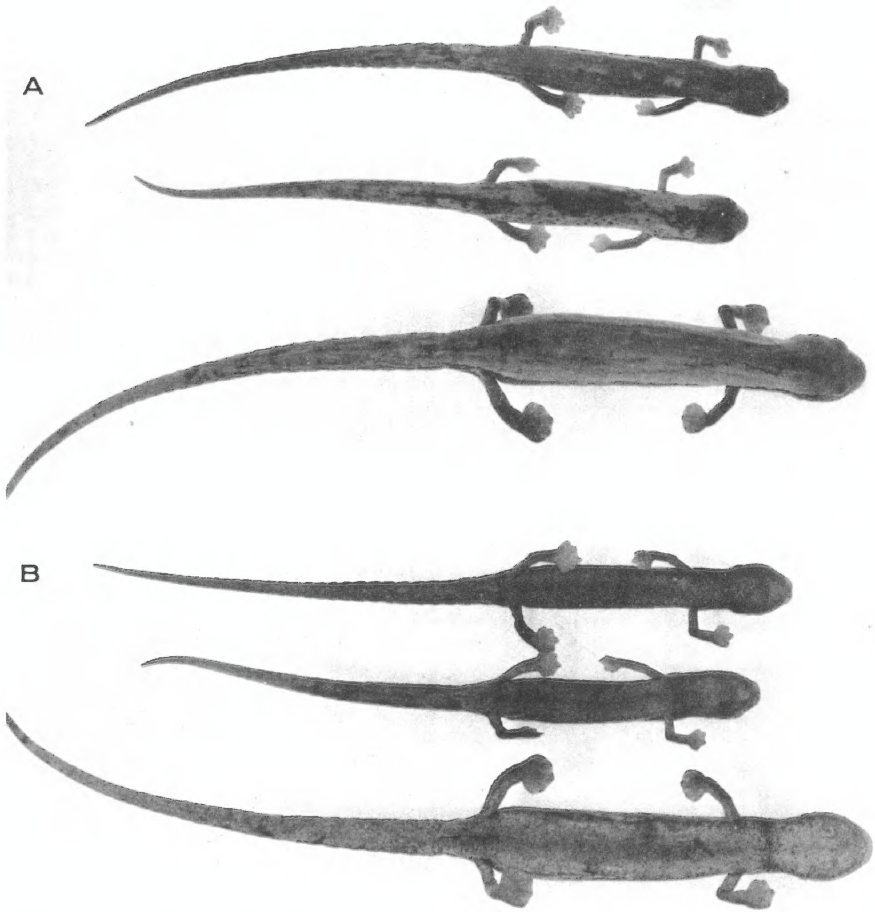


FIG. 3. Color pattern variation in paratype series of *Bolitoglossa taylori*. A. Dorsal aspect, reading from top (K.U. Nos. 116540, 116542, and 116545). B. Ventral aspect.

some (K.U. No. 116542) and merge with the dark dorsal color in others. One specimen has a very light, nearly cream-colored snout, with a sharp line of demarcation from the dark brown of the posterior part of the head at a point between the eyes. Ventral color varies from dark blackish brown in the dark animals cited above to very light in others. Punctate small guanophores are always present and, in addition, cream-yellow chromatophores are present in the lighter individuals. The lightest individual is the large female (K.U. No. 116545, see fig. 3B) which approaches the coloration of some *B. schizodactyla* in having a kind of ventral "enamel-

TABLE 1
DATA FOR THE TYPE SERIES OF *Bolitoglossa taylori* (MEASUREMENTS ARE IN MILLIMETERS)

	Museum number	Sex	Snout to Vent (Standard) Length	Axilla to Groin	Head Width	Snout to Gular Fold	Hind Limb Length	Tail Length	Foot Width	Number of Maxillary Teeth	Number of Vomerine Teeth	Costal Folds between Appressed Limbs	(Limb Interval)
K.U.	No. 116544 ^a	♂	53.3	28.4	8.9	13.3	12.9	55.9	5.8	76	32	2	2
G.M.L.-C.W.M.	No. 6077	♂	51.1	27.6	8.2	12.2	11.7	54.8	5.1	62	26	21	21
K.U.	No. 116540	♂	48.0	25.7	7.6	11.4	11.8	61.6	5.1	74	29	11	11
K.U.	No. 116542	♂	46.1	25.2	7.3	10.9	10.9	49.2	4.9	46	25	2	2
K.U.	No. 116535	♂	41.7	21.8	6.8	10.0	9.8	46.0	4.2	44	18	2	2
K.U.	No. 116543	♂	39.5	21.7	6.6	9.9	9.1	40.9	4.1	63	35	23	23
K.U.	No. 116545	♀	64.7	36.4	10.1	15.7	13.8	73.3	6.4	78	49	31	31
K.U.	No. 116539	♀	45.8	25.0	7.6	10.7	10.8	— ^b	4.8	57	36	3	3
K.U.	No. 116538	♀	42.0	22.9	7.3	10.8	10.5	50.6 ^b	4.2	55	37	2	2
K.U.	No. 116546	Juv.	38.4	21.3	6.4	9.8	8.8	—	3.7	47	23	21	21

^aHolotype.

^bRegenerated tail.

ing" of yellowish chromatophores overlying the darker ground color (cf. Wake and Brame, 1966). This color is not as intense as in *B. schizodactyla*, however. Hands and feet are lighter than limbs, and ventral surfaces of the appendages are lighter than are dorsal ones.

COLOR IN LIFE: The specimens were brighter and even more variable than indicated in the above description. The dorsal surfaces were light grayish brown, light brown, yellowish brown, orange-brown, or rich red-brown—sometimes with extensive dark brown or black dorsal markings, and often with a dark brown lateral stripe. One specimen had a conspicuously tan snout, and some individuals turned blackish on the tail. Ventral surfaces were light grayish brown, light yellowish brown, light orangish brown, or, usually, light brown. The venter always was speckled with white, and some individuals had a scattering of larger flecks of yellow. The coloration of the iris was in most cases light orange-brown, but was noted as light red-brown for one individual. There may be geographic significance in the fact that the latter specimen also was the only one having a "rich red-brown" dorsum (the venter was light brown). This specimen came from 1440 meters elevation near the middle of the Serranía de Pirre, whereas all other specimens were collected at 900–1100 meters on the northern end of the *serranía*.

OSTEOLOGY

All information has been obtained from radiographs. Skulls are large and well ossified, but not much detail can be seen. Typical features of the genus prevail, and our comments refer to characters subject to variation between species.

The vomers are separated on the midline and do not have any posteriorly directed medial processes. The preorbital processes of the vomers are long and extend well beyond the limits of the internal nares. Nasals are large and protuberant and extend far beyond the dorsal dental arcade. Small prefrontal bones seem to be present, but we cannot be sure of this. Ribs are present on all but the last trunk vertebra, but the last two pairs of ribs are very short. There are 1 cervical, 14 trunk, 1 sacral, 2 caudosacral, and a variable number (27, 36, 38, 39, 41, 42, in six individuals) of caudal vertebrae. Larger individuals have more tail vertebrae. The transverse processes of the first caudosacral vertebra extend nearly laterally and slightly posteriorly. The processes of the second are distinctly oriented anteriorly. The processes of the first caudal vertebra are oriented sharply anteriorly. These very large processes are not bifurcated and do not cross those of the second caudosacral vertebra. In the

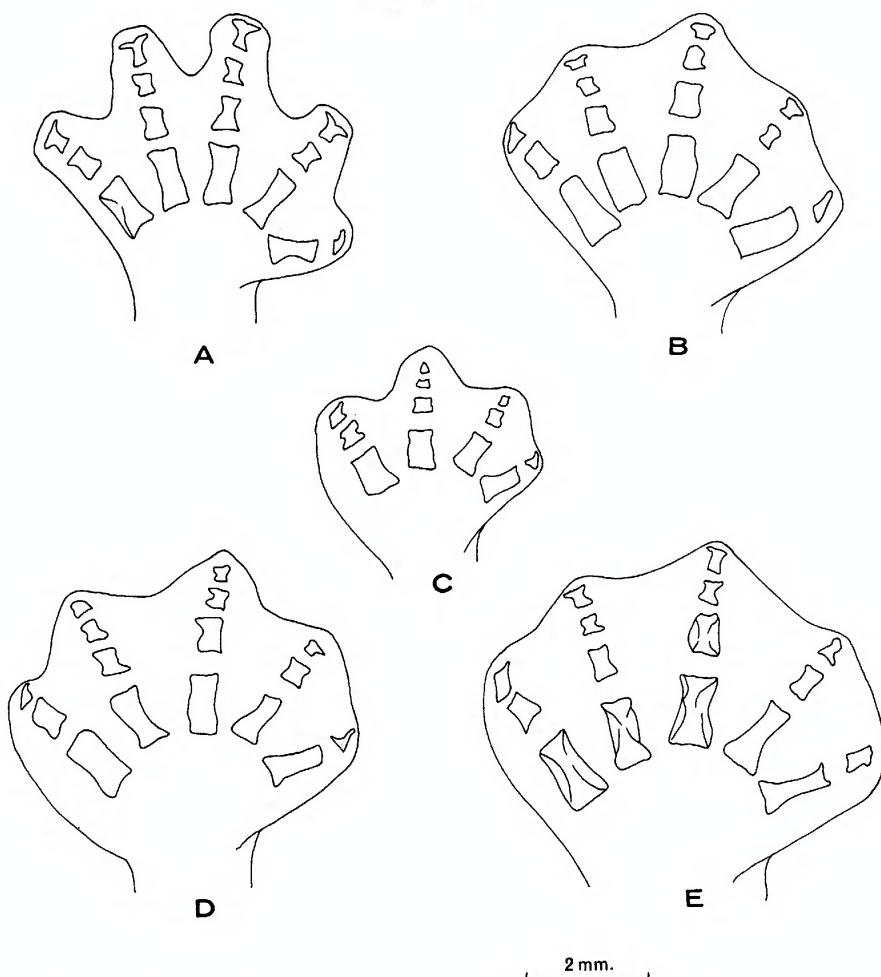


FIG. 4. Outlines of hands and feet and metapodials and phalanges, taken from radiographs. A. *Bolitoglossa valleculea*, L.A.C.M. No. 42285, left foot. B. *Bolitoglossa borburata*, U.M.M.Z. No. 113871, left foot. C. *Bolitoglossa taylori*, K.U. No. 116540, left hand. D. *B. taylori*, K.U. No. 116544 (holotype), left foot. E. *B. taylori*, K.U. No. 116545, left foot.

largest specimen transverse processes on the caudal vertebrae reach their highest development, and these are visible only on the first three vertebrae as very small spines oriented sharply anteriorly and lying at the anterior end of each vertebra. Well-defined neural crests are present, at least on the first few trunk vertebrae. There are no tibial spurs. Phalangeal formulas are 1-2-3-2 and 1-2-3-3-2. There is some digit

flattening and the metacarpals and metatarsals have some bony webs extending laterally from the shafts of the bones. Terminal phalanges are all well developed and tend to be expanded distally (see fig. 4C-E).

HABITAT AND DISTRIBUTION

Bolitoglossa taylori has been found only on the crest of the Serranía de Pirre, which is the highest and least dissected of three anticlinal fault blocks in extreme southeastern Panama (Myers, 1969, pp. 3-6). This *serranía* is aligned north to south and is about 35 kilometers long, rising rather abruptly at its northern end from the nearly base-leveled lowlands of the Río Tuira drainage, and essentially terminating on the Panamanian-Colombian border in a region of lower hills. It is fundamentally an unbroken ridge with a few prominent peaks, the highest being Cerro Pirre (1550 meters) near the middle of the ridge and Cerro Cituro (1110 meters) near the northern end. Ascending air currents cause nearly constant cloud formation along the crest of the ridge, even during the dry season. Although the ridgetop is quite narrow in places, and the soil is correspondingly thin, the high humidity and low rate of evaporation result in a luxuriant, epiphyte-laden cloud forest that is markedly different from the evergreen seasonal forest (monsoon rain forest) that blankets the slopes of the *serranía*.

All but one of the specimens were collected January 17-23, 1966, on the ridge north and south of Cerro Cituro, at elevations of 900-1100 meters. Four individuals were found at 900-1000 meters on the "north ridge," on two adjacent peaks (960 and 1000 meters) that sometimes are visible from the town of El Real in the lowlands north of the *serranía*. The ridgetop in this area is narrow and the cloud forest is low (canopy less than 18 meters) and exceedingly dense; the small tree trunks are choked with moss, bromeliads, and other epiphytes, and the herbaceous vegetation is abundant. An additional eight specimens from near Cerro Cituro were taken on the "south ridge" in the vicinity of a campsite at 1100 meters elevation. This is the type locality (fig. 5), which could be reached, after trail was cut, in about two and one-half hours from the northernmost of the aforesaid peaks. The ridge at this point is relatively wide and the soil sufficiently deep to support a forest having a moderately high canopy (more than 20 meters). The vegetation is more open than at narrower places on the ridge, but epiphytes are abundant on the trunks of trees, and there is a well-developed stratum of ferns and herbaceous broadleaf plants (fig. 5; Myers, 1969, fig. 12). Tree ferns are abundant, but palms in the understory are relatively

scarce. The cloud forest is strictly a ridgetop phenomenon at the type locality and elsewhere on the northern end of the *serranía*, as explained by Myers (1969, p. 23). Salamanders probably disperse out of the cloud forest to somewhat lower elevations, but it is doubtful if populations could be as dense, or even maintained at all, in the evergreen seasonal forest. The latter zone is at times very wet, but it also is subject to periods of relative dryness, especially on the well-drained, steep slopes



FIG. 5. Physiognomy of cloud forest, 1100 meters elevation, at type locality of *Bolitoglossa taylori* (January 24, 1966). Most salamanders were found on such herbaceous vegetation at night, but by day some were hidden in bromeliads on tree trunks.

and particularly during the long, dry season that lasts from about late December to early April. Correlated with this, but perhaps of more importance to the salamanders, is the near lack of suitable epiphytic growth in which these arboreal animals can hide and remain moist by day, and the greatly decreased density of herbaceous plants on which they can prowl by night. These factors make it seem likely that *Bolitoglossa taylori* is confined almost to the very crest of the northern part of the *serranía*, or, at the very least, that the maximum population density is in the ridgetop cloud forest.

The middle part of the Serranía de Pirre, at Cerro Pirre itself, is

higher, and the cloud forest consequently develops at a greater elevation. Cloud forest first occurs between 1300 and 1400 meters and extends to the top at 1550 meters. The forest is lush and wet as on the northern end of the *serranía*, but temperatures are cooler and bromeliads are abundant on the ground as well as on trees. Only one salamander was obtained here, near a campsite at 1440 meters, on May 25, 1965. It was pigmented somewhat differently than the specimens collected farther to the north (see Color in Life).

Bolitoglossa taylori thus occurs on the northern half of the Serranía de Pirre, and very probably it inhabits the entire length of the ridge. The ecological conditions commented on above, and the frequent tendency for montane *Bolitoglossa* to be geographically restricted, raises the possibility that *B. taylori* is endemic to the isolated cloud forest on the Pirre ridge. This is only speculation, of course, as too few salamanders have been collected in eastern Panama and adjacent Colombia for definitive statements about range. Nonetheless, it is interesting that Myers did not obtain *B. taylori* by using the same collecting techniques in a cloud forest (730–960 meters, Jaqué-Imamadó divide) situated no more than about 30 kilometers southwest of the Serranía de Pirre, in the Cordillera de Juradó (Myers, 1969, figs. 1, 11). Two different species of *Bolitoglossa* occurred there, namely *B. phalarosoma* and an undescribed species. Specimens of additional species are known from the Darién lowlands, but *B. taylori* is not among them.

BEHAVIOR

Bolitoglossa taylori is nocturnal as are most, if not all, other members of the genus. Also, it is arboreal, as is characteristic of the forest-dwelling species of *Bolitoglossa*, which live at moderate to low elevations. Four individuals were found by day, in bromeliads on the sides of trees. The other specimens were abroad by night, sometimes during rain. One juvenile was on vegetation only several centimeters above ground. Eight others were on leaves and branches $\pm$ 1 meter above the forest floor. In most cases they were motionless when first seen. Any subsequent movement was sluggish until they were prodded during capture.

The male and female shown in figure 1 were found on the same leaf roughly a meter above ground on the night of January 23, 1966. They faced in the same direction, the female lying behind the smaller male, with her head resting on his tail. Evidently disturbed by the beam of the headlight, they moved apart. They were kept alive in the same container for a day or so, but exhibited no other behavior of note.

RELATIONSHIPS

Bolitoglossa taylori is similar to members of the *adspersa* group, which includes nine South American species (Brame and Wake, 1963). This group has not been formally defined, and it will eventually be subdivided further. A core assemblage containing *B. adspersa*, *B. valleculea*, *B. savagei*, and *B. borburata* is fairly distinctive, and the last three species seem to be close relatives. *Bolitoglossa valleculea* of the Cordillera Central of Colombia, is the most generalized of these three species. It is an upland form (above 1900 meters) with little webbing and large, distinct digits (fig. 4A) with subterminal pads. *Bolitoglossa savagei*, from the Sierra

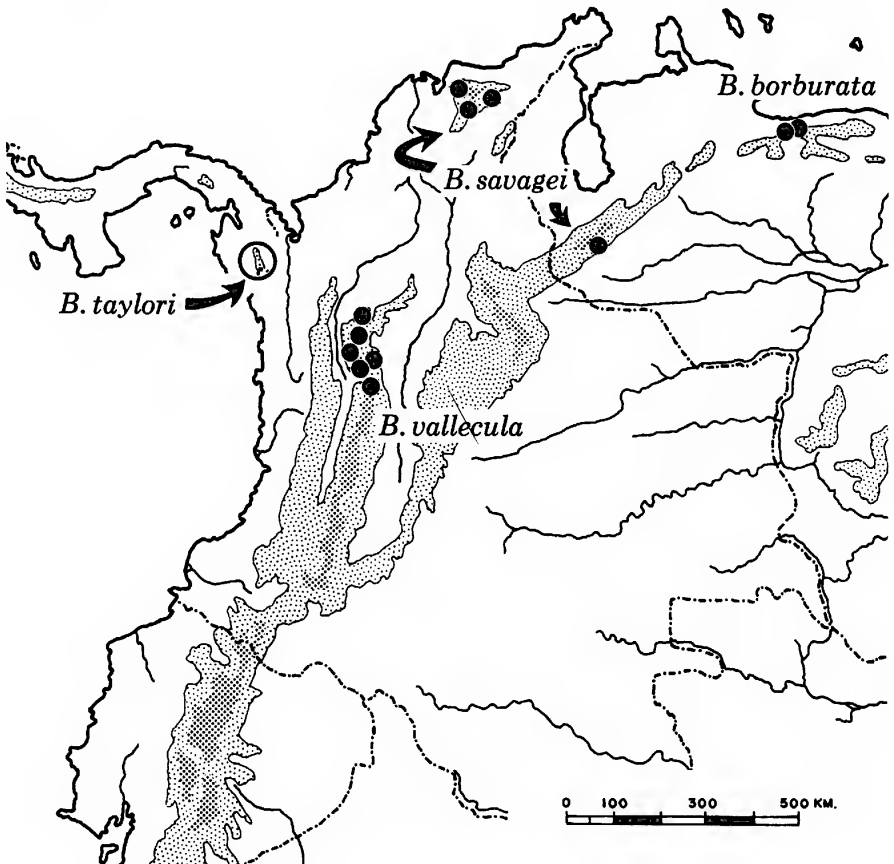


FIG. 6. Map of northern South America and Panama, indicating montane distributions of *Bolitoglossa taylori* and its relatives. Light and dark stipple patterns denote elevations above 1000 and 3000 meters, respectively.

Nevada de Santa Marta in north-coastal Colombia, occurs at elevations between 1000 and 2100 meters. It has more webbing than *B. valleculea* but retains distinct, knoblike digital tips and large subterminal pads. *Bolitoglossa borburata*, from the Cordillera de la Costa of northern Venezuela, is known to range between 1000 and 1200 meters. It has more webbing and less distinct digits than those of the other species (fig. 4B); the digital tips are rounded to slightly pointed, flattened, and lack subterminal pads.

Bolitoglossa taylori, which occurs between 900 and 1440 meters, resembles the above species, especially *B. borburata*. *Bolitoglossa borburata* and *B. taylori* are of similar size and have legs of similar length. Both have relatively many maxillary teeth. *Bolitoglossa taylori* has more vomerine teeth, a slightly broader head, slightly more webbing of the hands and feet, and subterminal pads. The two species are very similar, however.

In addition to having less webbing of hands and feet and more prominent digits, *B. savagei* tends to have fewer vomerine and slightly fewer maxillary teeth than those of *B. taylori*. In most other features, including head width, leg length, and general habitus, the species are very similar. The largest male and female of *B. taylori* are longer than the largest known members of the same sex of *B. savagei*, *B. borburata*, and *B. valleculea*, but mean sizes are similar in the four species.

The hands and feet of *B. valleculea* have the most prominent digits and the least amount of webbing of the group, and these features distinguish the species from *B. taylori*. *Bolitoglossa valleculea* is also distinguished from *B. taylori* by its light yellowish or pinkish ventral coloration, far fewer maxillary and vomerine teeth, and a tendency to have a slightly narrower head.

Brame and Wake (1963) suggested that *B. valleculea*, *B. savagei*, and *B. borburata* formed a series of related species derived from an ancestral stock that also gave rise to *B. adspersa*. *Bolitoglossa valleculea* was considered to be the most generalized and primitive, and *B. borburata* the most derived, with *B. savagei* somewhat intermediate between the two. *Bolitoglossa taylori* also fits into this series, and in terms of relative degree of derivation would lie between *B. savagei* and *B. borburata*. Because we have so little information concerning some of the species, especially in regard to osteological data, our statements concerning degree of derivation must be viewed as tentative. We have tended to emphasize the structure of the hands and feet, for elsewhere in the genus increase in webbing, decrease in digit individuality, increase in foot flattening, and loss of subterminal pads are all derived features. The four species under consideration can be arranged in a series, from primitive and generalized

to derived and specialized, according to hand and foot structure as follows: *B. valleculea*, *B. savagei*, *B. taylori*, *B. borburata*. This arrangement also correlates with a decrease in altitudinal range, with the last two species occurring at the lowest elevations.

Certain other trends are evident in the sample. Maxillary teeth increase in number from *B. valleculea* (28–61, mean 44; N = 16) to *B. savagei* (23–79, mean 48; N = 31) to *B. borburata* (49–71, mean 57; N = 11) to *B. taylori* (44–78, mean 60; N = 10). Vomerine teeth increase in number from *B. valleculea* (14–24, mean 19; N = 20) to *B. savagei* (13–33, mean 23; N = 30) to *B. borburata* (18–33, mean 24; N = 12) to *B. taylori* (18–49, mean 31; N = 10). Snouts tend to be somewhat longer in *B. borburata* and *B. taylori*, especially in females, but our samples are too small to document this observation. Mean ratios of snout–gular fold length to standard length are as follows: *B. valleculea* males 23.6, females 21.5; *B. savagei* males 23.5, females 22.5; *B. borburata* males 24.1, females 23.1; *B. taylori* males 24.3, females 24.5. Heads tend to be slightly broader in *B. taylori* than in the other species, and *B. valleculea* has the narrowest head. A tendency for a dorsal light band is seen in all of the species, but especially in *B. borburata*.

Based on the above characters, we suggest that *B. taylori* and *B. borburata* are close relatives and that they have been derived from an ancestral stock that might have been similar to *B. savagei*. *Bolitoglossa valleculea* is less similar to *B. taylori* than are the other two species, and we believe that it is also not so closely related. In addition to the structural evidence concerning relationships, the distributional pattern (fig. 6) of disjunct populations in isolated upland situations is what one might expect for a group of closely related species.

The correlation between foot structure and elevation is striking in this group, with the two species of relatively low elevations (*B. taylori* and *B. borburata*) having the greatest webbing and the least distinct digits. This pattern has been seen in species groups of *Bolitoglossa* in Costa Rica (Wake and Brame, 1963) and Guatemala and Mexico (Wake and Brame, 1969), as well as South America. The genus *Bolitoglossa* has the most extensive continuous range of any salamander. Within this vast range, species groups tend to be localized, and a persistent pattern is found in which relatively primitive species occur in the uplands, mainly in terrestrial situations, and derived species occur in the lowlands, mainly in arboreal situations. Among the lowland derived species, the ones in the northern and western parts of the range tend to be more primitive than those in the southern and eastern parts.

Two Panamanian species, *B. biseriata* and *B. schizodactyla*, show some

similarities to *B. taylori*, but it is unlikely that either is a close relative. Some small individuals of *B. taylori* are very similar to some large *B. biseriata*, especially in coloration. *Bolitoglossa biseriata* is smaller, has fewer teeth, and has more extensively webbed feet with less distinctive digits and no subterminal pads. The type locality of *B. biseriata* is at a lower elevation (less than 100 meters above sea level) but is only about 22 kilometers from Cerro Cituro. *Bolitoglossa schizodactyla* is a larger species which is not known to occur in Darién. It has distinctive hands and feet (Wake and Brame, 1966) with expanded, highly specialized terminal phalanges and much webbing. Some individuals have coloration that is similar to that seen in some *B. taylori*, but in most features the species are very distinct. In addition to the other distinguishing features, *B. schizodactyla* has more teeth and longer legs than those of *B. taylori*.

Other Panamanian species are not likely to be confused with *B. taylori*. *Bolitoglossa colonnea* has a distinctive dermal interorbital boss and no maxillary teeth. *Bolitoglossa lignicolor* is a larger species with fewer teeth; it has extensively webbed feet that lack subterminal pads, but the feet are quite distinctive in being relatively thickened. *Bolitoglossa marmorea* is larger and has much less webbing and more discrete digits. Other Panamanian and Colombian species will be discussed more fully in forthcoming publications.

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